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Substratum-Associated Microbiota

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Substratum-associated microbiota

Christopher G. Peterson, Nancy C. Tuchman

METHODS

Lamberti (1993) produced a useful review of 31 benthic algal/macroinvertebrate herbivore experiments conducted in artificial streams. He discussed the advantages associated with using artificial streams for such studies (for example, relative ease of manipulating macroinvertebrate grazers, periphyton, and environmental factors) and their limitations, including departure from realism of natural ecosystems.

Some varied approaches to explaining the complexities and variation among benthic communities were proposed. Cattaneo *et al.* (1993) suggested that highly variable periphyton assemblages can be modeled more accurately by including measurements of physical, biological, and chemical factors; by considering microscale variation; and by partitioning periphyton into functional groups. Clarke and Ainsworth (1993) argued that canonical correlations are inappropriate for linking observed community structure to measured environmental variables and proposed a simple rank-order/ordination technique, which they illustrated with three benthic community data sets. Cox (1993) advocated the integration of results from culture experiments that test the growth of diatom populations under various conditions (for example, light, temperature, and pH), with field observations of these diatoms to aid in interpreting their distributions in nature.

Methods of preparing, extracting, and determining benthic chlorophyll *a* concentrations were described by several authors. Plante-Cuny *et al.* (1993) compared spectrophotometric measures of chlorophyll *a* to high-pressure liquid chromatography (HPLC) measurements of 57 marine coastal sediment samples and found that, although both methods provide reliable chlorophyll *a* estimates, spectrophotometry requires less time and effort. Redden *et al.* (1993) examined the effects of freezing samples on chlorophyll-*a* type algal pigments. Freezing temperature (-196°C , -79°C , or -20°C) had no effect on total pigment recovery from samples stored for 1 day, and long-term freezing showed that degradative effects were most pronounced within the first week of storage.

Some methods for collection, identification, and enumeration of substratum-associated microbiota were proposed. Davies and Gee (1993) developed a simple periphyton sampler consisting of a short length of wooden broom handle and a disposable scouring disc that they suggest is significantly more efficient at removing and retaining periphyton from stones in streams than other commonly used techniques. A similar device was designed by Snoeijns and Snoeijns (1993) that requires the stone substratum to be lifted from the water before sampling attached algae. Scholz and Boon (1993a) described a technique for submerging wood in the photic and aphotic zones of lentic environments and described assays for activity of alkaline phosphatase, beta-D glucosidase, and aminopeptidase enzymes associated with biofilms that colonized these substrata. Costas *et al.* (1993) used fluorescein isothiocyanate-labeled lectins to identify and differentiate between clones of the same species of unicellular algae and to discriminate between phylogenetically closely related species. Ward and Cockcroft (1993) developed a strain-specific immunofluorescence assay for enumeration of a marine denitrifying bacterium, *Pseudomonas stutzeri*, in the water column and within marine microbial mats. Plante and Jumars (1993) used a similar immunofluorescence assay to study feeding, digestion, and egestion of a marine deposit feeder, *Abarenicola pacifica*, on a naturally occurring pseudomonad population and were able to document preferential ingestion of the bacteria by comparing relative abundance of pseudomonads in the sediments with that in the animal's foregut. Gasol (1993) presented a dilution technique, followed by live enumeration that allows accurate density estimates of sparse protist populations from fine sediments to be made. Mitchell *et al.* (1993) developed a method to extract single bacterial cells from a complex microbial assemblage for isolation purposes using a nondestructive laser beam.

Methods of estimating and assessing bacterial activities in benthic habitats were published. Johnson and Ward (1993) reported that a modified filter-transfer-freeze procedure was useful in detecting iodinitrotetrazolium formazan (INT) crystals in unattached bacteria but that this technique did not enhance detection of INT crystals in particle-bound benthic bacteria. Further, they found no significant differences in INT crystal detection between prestained polycarbonate filters mounted with immersion oil and those mounted with glycerol but that, in immersion oil, crystals were still evident within bacterial cells even after 24 hours. An acid-extraction method to determine the contribution of bacterial processes to phosphate uptake in sediments was described, and experimental results indicated that the bacterial contribution ranged from 12 to 32% (Sinke *et al.*, 1993). Chrzanowski *et al.* (1993) empirically determined the conversion factors needed to estimate bacterial growth rates from

rates of thymidine incorporation into DNA. To accomplish this, they compared changes in bacterial cell numbers over time to growth-rate constants estimated from empirically derived, theoretical, and modeled conversion factors.

Pickney and Zingmark (1993a) examined the photosynthetic response of benthic microalgal communities from different light environments (unshaded mudflats versus highly shaded *Spartina* stands) with traditional depth-integrated methods as well as with percent P_{\max} and fixed-depth interval methods. They concluded that a fixed-depth interval method provides a more realistic representation of the photophysiological responses of these communities.

ECOLOGY

Colonization and community development. The influence of hydrodynamic conditions on the development of attached microbial communities was examined by several authors. Hoffmann (1993) described the design, advantages, and disadvantages of laboratory microstreams as a tool to study benthic microalgal immigration and emigration in lotic systems. He suggested that such a system, when linked with field studies, could prove valuable in understanding benthic algal dynamics in natural systems. Rijnaarts *et al.* (1993) found that suspended bacteria were able to attach to solid substrata more efficiently under dynamic flow conditions (in which convective forces and diffusion were at work) than under conditions of static (diffusion alone) flow. Under static-flow conditions, bacteria tended to exhibit greater resistance to removal by shear stress when adhering to Teflon surfaces than when attached to glass. Short-term (<100 hour) biofilm-accumulation experiments conducted by Lau and Liu (1993) suggested that, for thin bacterial biofilms, cell accumulation rates were most rapid at slow current velocities (<3.5 $\text{cm} \cdot \text{s}^{-1}$) compared with faster flows (>10 $\text{cm} \cdot \text{s}^{-1}$).

Liu *et al.* (1993) used sequential acid hydrolysis and HPLC analysis to argue that the origin and mass of a biofilm developed for ≤ 26 hours in both indoor and outdoor seawater-fed stream systems was derived, primarily, from the activity of attached bacteria rather than algae. These authors noted detectable (in terms of total carbohydrate) attached bacterial biomass in outdoor channels after 1 hour but found significant differences between biofilms incubated in indoor versus outdoor experimental channels. Ács and Kiss (1993a) monitored diatom colonization on sand-blasted glass slides in the River Danube over a 6-month period and identified three phases of species compositional change, from an early successional stage dominated by large araphid and biraphid taxa to a midsuccessional stage characterized by small bi- and monoraphid species to later collections dominated by medium-sized mono- and biraphid diatoms. Stewart (1993) presented a model to allow better prediction of sloughing patterns in attached biofilms. His model incorporated detachment caused by changes in cell condition along gradients of resource availability that exist, with depth, in natural biofilms. Rittmann (1993) argued that the pattern of spatial distribution of bacterial biofilms is determined by the substrate loading in a system; for low loading rates less than ca. 0.038 kg chemical oxygen demand $\cdot 1\,000\text{ m}^{-2} \cdot \text{d}^{-1}$, formation of discontinuous biofilms is likely.

The effect of substratum size and distance from a colonization source on colonization patterns of ciliated protozoa in microcosms was examined by Have (1993). Results of this study sug-

gested that spatial variability in substratum availability and interspecific differences in dispersal abilities among ciliates allow global coexistence of a large number of species.

Several authors investigated colonization, distribution, and effect on the host of epizoic algae attached to microcrustaceans. Gaiser and Bachmann (1993) reported that only 35% of 62 north temperate lakes and marshes surveyed contained cladoceran assemblages that supported epizoic algae; cladocera in the systems in which epizoic algae occurred were dominated by *Daphnia* spp. Epizoic algal assemblages were comprised of 49 taxa but were dominated by the diatom *Synedra cyclosum*; densities averaged 119 cells $\cdot \text{animal}^{-1}$ and were highest immediately after ice-out when cladoceran molting rates were low. Extremely high densities of *S. cyclosum* (22 900 cells $\cdot \text{animal}^{-1}$) increased sinking rates and mortality rates in two species of *Daphnia* in Lake Mendota (Allen *et al.*, 1993). Threlkeld and Willey (1993) reported that epizoan load on *Daphnia* in two subalpine beaver ponds was proportional to microcrustacean body size and that, of the three algal genera studied, only *Colacium* negatively affected cladoceran egg production. Different genera of microcrustacea support different epizoic assemblages; algal attachment is site-specific and does not result from any interaction between epizoic species (Willey and Threlkeld, 1993).

Temporal and spatial distribution. Carpenter and Williams (1993) measured differences in flow velocity profiles over marine algal turfs of different heights and microtopographies and suggested that such variation in flow patterns should translate to microscale variation in primary productivity. Biggs and Gerbeaux (1993) sampled periphyton weekly for a year from six sites on two New Zealand rivers to assess the relative importance of in-stream discharge patterns compared with large-scale catchment characteristics in dictating biomass and structure of benthic algal communities. Discharge variation explained much of the month-to-month variation in algal biomass, whereas among-system differences in mean chlorophyll *a* biomass over the year was tied more closely to geology and land use within catchments. Hax and Golladay (1993) noted that microbial biomass accrued to higher levels on wood substrata than on leaves in both fast- and slow-current habitats in a boreal river; this was one factor likely responsible for higher macroinvertebrate densities they observed on wood. Spatial variability in bacterial production, turnover time, and responsiveness to enrichment by organic carbon in the hyporheic zone of a northern Michigan river was tied to patterns of hydrologic exchange between the surface stream, hyporheic, and groundwater (Hendrick, 1993).

McCormick (1993) examined longitudinal linkages in lotic communities in an artificial stream and demonstrated that invertebrate grazing activity in upstream channel sections could increase algal accumulation on initially barren substrata downstream. Upstream grazing activity had no apparent effect on algal abundance in established downstream communities. Leff *et al.* (1993) found that Gram staining and bacterial cell morphology were useful in distinguishing among bacterial cells from different source pools in lotic systems. Using this system, they were able to demonstrate a storm-induced influx of bacteria from floodplain soils into a stream.

The degree of interconnectivity between phytoplankton assemblages and assemblages of benthic algae in lake systems was examined in two separate studies. Hansson (1993) reported that the mechanism behind the shift from benthos to water column exhibited by many algal taxa varies on a taxon-specific basis,

but this shift is probably not driven by wind- or temperature-induced turbulence. Rodriguez (1993) found little taxonomic overlap between the phytoplankton assemblage in a temperate oligotrophic lake and algae attached to plexiglas plates collected over a 12-week incubation period or on plates exposed for successive week-long intervals over the course of the study.

Two studies examined the spatial and temporal variation in dissolved nutrient concentrations and benthic primary producers in tropical floodplain systems. Engle and Melack (1993) tracked changes in dissolved nutrients, in biomass of epiphytic algae on "floating meadows" of macrophytes, and in phytoplankton biomass during periods of riverine flow, floodplain inundation, and transitions between these states. Epiphytic algal biomass was highest during lentic-to-lotic transitions. *In situ* bag experiments revealed that turbidity of river water limited algal ability to use dissolved nutrients. Vegas-Vilarúbia and Herrera (1993) reported that two permanent Venezuelan floodplain lakes were autotrophic, but a transient lake created when the Mapié river expands during the rainy season was primarily heterotrophic. Net and gross primary production in the transient lake showed no clear spatial pattern, reflecting a mosaic of different biochemical states.

Ács and Kiss (1993b) attempted to relate the intermediate disturbance hypothesis to periphyton abundance and diversity on glass plates in the River Danube. They reported a negative correlation between discharge and algal densities and that these changes complexly influenced diversity. Given such variability in natural systems, Steinman (1993) discussed the advantages, disadvantages, uses, and abuses of using artificial stream channels to study disturbance effects on periphyton.

Madsen *et al.* (1993) used an experimental flume system and light manipulations to demonstrate that variation in the stability of subtidal sediments could be attributed to growth of benthic algae and, presumably, their associated extracellular polysaccharides. Bacterial biomass on submerged wood in an Australian billabong was greater on wood placed in the photic zone than in the aphotic zone of this system (Scholz and Boon, 1993b). An analysis of phospholipid fatty acids (PLFA) in these biofilms showed distinct differences between PLFA profiles in summer and winter but no clear light-regime effects. Schallenberg and Kalff (1993) analyzed bacterial-abundance data collected from sediments at 46 lake sites, along with similar data from an additional 98 sites obtained from nine previously published studies to determine the most important factors determining distribution of sediment bacteria in aquatic ecosystems. The abundance of sediment bacteria was strongly influenced by the amount and C:N ratio of organic matter in sediments, and, in lakes, was affected by sediment water content, hydraulic flushing rate, and whether sediments were overlain by hypolimnetic or epilimnetic water. Distributional patterns of benthic nanoflagellates with depth (deep, >1 000 m; shelf, 10 to 100 m), upwelling, and sediment grain size in a marine coastal area were described by Bak and Nieuwland (1993). Flagellate densities were most influenced by grain size, and heterotrophic nanoflagellates increased in nonupwelling areas. Hawes *et al.* (1993) reported that distribution and abundance of benthic cyanobacterial mats in Antarctic ponds is determined by the effect of years of accumulation and that these communities act as a significant sink for inorganic nutrients. A study of the nitrogen and carbon dynamics of perennial cyanobacterial/diatom mats in the outflow stream of an Antarctic lake showed these communities were highly stable,

with N:P ratios similar to stream water, and carbon and nitrogen uptake balanced with loss (Davey, 1993).

Peterson *et al.* (1993c) described the effects of a bacterial pathogen on dense, rapidly growing benthic diatom communities in a desert stream during two successive infection periods. These infections spread outward from discrete points of origin on the benthos, presumably via cell-to-cell contact, and significantly altered diatom community structure and biomass. Sabbe (1993) simultaneously tracked diatom abundance and taxonomic structure in epipellic and epipsammic assemblages in a brackish-water intertidal sandflat and reported that epipellic assemblages increased significantly in response to changes in light regime and sediment organic-matter content, whereas epipsammic communities showed no clear change. Highest densities and diversity of benthic macroalgae in a Brazilian river occurred during periods of low flow, low turbidity, and cooler temperature (Necchi and Pascoaloto, 1993). Benthic macroalgal communities in an Austrian stream exhibited considerable spatial variation in taxonomic content at any given time, but seasonal dynamics in this system were most influenced by flood regime (Pfister, 1993). Goldsborough (1993) tracked seasonal changes in vertical microspatial distribution of epiphytes (primarily diatoms) on extensive floating mats of common duckweed in ponds and marshes of western Canada. Extreme spatial and temporal variation in temperature in these mats, along with sharp vertical profiles of dissolved oxygen and nutrients, limited the number of diatom species that can colonize this habitat. Gosink *et al.* (1993) studied the vertical distribution of bacteria in sea ice microbial communities off Point Barrow, Alaska, and found bacterial densities to be greatest in the vertical layer containing highest chlorophyll *a* concentrations; the occurrence of psychrophilic gas vacuolate bacteria was reported for the first time in arctic sea ice communities.

A number of studies examined differences in microalgal distribution among systems of varying chemical characteristics. Taxonomic diversity and species richness of benthic diatoms decreased among Polish streams along a gradient of decreasing pH, and species-specific changes associated with the pH gradient were noted (Kwandrans, 1993). Kinross *et al.* (1993) analyzed the distribution of 49 taxa of filamentous algae over 3 years in 10 Scottish streams with respect to physical and chemical habitat characteristics, particularly pH. Although no clear relationship between algal standing crop and pH was found, ordination of the data revealed that pH or pH-related variables explained much of the variation in macroalgal community structure among these systems. John (1993) monitored changes in benthic and planktonic diatom flora during conversion of former sand-mining pits to created wetlands. The conversion raised pH and increased nutrient concentration in these systems, increasing diatom diversity and generating a significant shift in community structure. The structure of benthic diatom communities among 62 saline lakes distributed across a wide range of latitudes in western North America varied along gradients of specific conductance and concentrations of major anions (Blinn, 1993). pH and major cations proved to be of little predictive value, suggesting that diatoms are more sensitive to variation in pH from acidic to neutral rather than the near-neutral to basic. Jones *et al.* (1993) analyzed data from 59 Antarctic lakes and found that among-lake differences in benthic diatom species composition were strongly related to gradients of water column nutrients and salinity.

Seasonal variation in the structure and production of protistan communities in three sandy beaches on the Sea of Cantabria was described by Fernandez-Leborans and Novillo (1993). These authors provided a detailed taxonomic treatment of this group. Schmid-Araya (1993) studied spatial (longitudinal and with sediment depth) and temporal (over a year) changes in abundance and reproductive activity of the bdelloid rotifer, *Embata laticeps*, in a gravel-bed stream. Seasonal changes in abundance and reproductive activity of microcrustacea from three Welsh streams of contrasting pH were reported by Rundle (1993). pH-related variation in reproductive output was noted for some species. Peak densities of microcrustacea occurred at all sites in late summer/autumn, but this resulted from increases in just a few taxa.

Kawecka and Olech (1993) described the taxonomic structure of diatom communities in two Antarctic streams and discussed the distribution of 74 taxa they encountered with respect to apparent ecological tolerances. The taxonomic composition of the diatom assemblage growing at a 35-m depth on the North Carolina continental shelf was described by Cahoon and Laws (1993). This microflora, which had not been well studied, was compared with algal assemblages from littoral sediments of this area and to planktonic assemblages. Sheath *et al.* (1993a and b) published on the systematics and distribution of North American representatives of two families of freshwater Rhodophyta, the Ceramiales, a group limited primarily to tropical waters of Central America and the Caribbean (a) and the genus *Batrachospermum* within the Batrachospermales (b). Treatment of the latter group included a description of a new species.

Herbivory. Several studies investigated interactions among abiotic resources, primary producers, and herbivores. Junger and Planas (1993) used stable carbon isotopes to test the hypothesis that benthic algal proliferation under acidic conditions results from lower grazing pressure. Rosemond (1993) manipulated irradiance, nutrients, and grazer densities in a small forested stream and demonstrated that nutrients and light had positive effects on algal biomass, whereas grazing had negative effects. Effects of these factors in combination, however, often differed from the effects of single factors alone. In a similar set of experiments, Rosemond *et al.* (1993) showed that nutrient addition positively affected both algal biomass and the growth of herbivorous snails. Hootsmans *et al.* (1993) investigated the interactions between periphyton density and shading in relation to tidal depth and grazing by fiddler crabs in intertidal seagrass beds. They suggested that periphyton accumulation and fiddler crab grazing pressure increased with tidal depth. Neckles *et al.* (1993) and Williams and Ruckelshaus (1993) both investigated the individual and interactive effects of nutrient enrichment and activity of epiphyte grazers on the epiphyte loads on eelgrass and on the growth of this marine macrophyte. Williams and Ruckelshaus documented complex interactions among sediment and water-column nutrient supplies, epiphyte loads, and grazing activity and argued that all of these factors must be assessed to gain an understanding of the dynamics of eelgrass productivity. Neckles *et al.* reported that effects of grazers on epiphytes were typically stronger than nutrient effects and that the nature of the interactions among these components and macrophyte growth varied seasonally.

Multiple trophic-level interactions were studied by Walters and Moriarty (1993) in a marine sediment community. The effects of meiofauna and protist density on bacterial numbers and microalgal-division rates varied with season, microbial

groups, and vertical positions within the sediment. Vaughn *et al.* (1993) investigated the trophic interactions among the algivorous minnow, *Camptostoma anomalum*, two invertebrate grazers (the crayfish, *Orconectes virilis*, and the snail, *Physella virgata*), and periphyton in recirculating streams. They suggested that crayfish were negatively affected by *Camptostoma* via direct competition for filamentous algae, whereas *Physella* benefitted from the removal of overstory algae by the minnow. Activity of atydid shrimp in a small, headwater, tropical stream was found to play an important role in stream recovery after high discharge events. These shrimp rapidly removed sediments and detritus from benthic substrata, enhancing growth of attached microalgae and facilitating exploitation of benthic algae by vagile grazers, like mayflies (Pringle *et al.*, 1993). Fitzgerald and Gardner (1993) estimated the magnitude of pelagic-benthic energy coupling in Lake Michigan using an algal carbon budget. The diatom, *Melosira*, accounted for 53% of the algal C flux to the sediments, 61% of which was subsequently assimilated by *Diporeia*, a benthic amphipod, and 2% was assimilated through microbially mediated algal decomposition. Robles and Robb (1993) reported that the persistence of red-algal turfs off Santa Catalina Island is dependent on the presence of predators (for example, spiny lobsters, carnivorous fishes, and whelks) that maintain low *Mytilus* (mussels) densities. Interactions between predators and mussels were mediated by wave activity.

Sarnelle *et al.* (1993) used a geostatistical analysis to examine how different intensities of snail grazing affected spatial heterogeneity in benthic algal communities in artificial streams. Grazing effects on spatial arrangement of overstory algae (*Cladophora* and epiphytes) differed from those measured in the algal understory. Botts (1993), in studying the impact of chironomid grazers on epiphytic algal abundance and dispersion, demonstrated that chironomids reduced the biovolume of preferred algal species, both via direct ingestion and through case-building activity, while increasing the degree of clumping of nonpreferred species. Field enclosure experiments showed that influences of chironomid grazing varied seasonally.

Effects of nutrients on microbenthos. Bothwell (1993) discussed the factors that should be considered and accounted for when using artificial streams to investigate microalgal/nutrient interactions. Stevenson and Glover (1993) used periphyton communities of different densities established on glass-fiber filters to demonstrate that increases in current velocity increased the vertical flux of dissolved nutrients ($\text{NO}_3\text{-N}$, silicon) and non-nutrient (chlorine) ions through periphyton mats. Nutrient flux was inversely related to periphyton density, indicating the effects of biological uptake, whereas transport of chlorine was impeded only at the highest algal densities, indicating physical interference of diffusion by the periphyton matrix.

Enrichment experiments were conducted on periphyton communities in a wide range of aquatic systems. A study of the individual and interactive influences of light, nitrogen, and phosphorus on attached algal biomass and species composition in a large oligotrophic lake (Flathead Lake, Mont.) revealed that nitrogen addition significantly increased algal biovolume and phosphorus stimulated growth only when added together with nitrogen; light manipulation had no effect on algal biovolume but did apparently influence diatom species composition (Marks and Lowe, 1993). Fong *et al.* (1993) manipulated nutrient concentrations at different ratios of N:P during two microcosm experiments, one in summer, one in spring, to assess the relative

importance of each of these nutrients in limiting algal biomass in a coastal lagoon. Nitrogen limitation was more prevalent in summer than in spring; complex interactions among components of these communities influenced enrichment response. Results of a nitrogen/phosphorus/carbon enrichment experiment conducted by Niederhauser and Schanz (1993) in an oligotrophic lake in the Swiss alps showed that carbon addition significantly influenced algal biomass but nitrogen and phosphorus addition had little effect. Fairchild and Sherman (1993) conducted nitrogen/phosphorus/carbon enrichment experiments in 12 softwater lakes of varying acidity and examined the structure of natural algal communities with respect to water chemistry parameters to determine the role of nutrients in structuring periphyton communities in these systems. Species composition was strongly related to pH and alkalinity and was relatively unaffected by dissolved nitrogen and phosphorus in the water column. The identity of the limiting nutrient varied, in contrast, with water-column nutrient concentrations and differed among species. Hürlimann and Schanz (1993) examined the response of riverine periphyton grown in artificial stream channels to prolonged (47-day) enrichment with different concentrations ammonium. Addition of $1.2 \text{ mg NH}_4\text{-N}\cdot\text{l}^{-1}$ had little effect on diatom community structure, but biomass reductions and dramatic changes in community composition to species tolerant of organic pollution occurred with addition of higher concentrations ($>5 \text{ NH}_4\text{-N}\cdot\text{l}^{-1}$). Injection of nitrified wastewater effluent into the groundwater close to littoral sediments of Lake Taupo, New Zealand, cause a localized increase in periphyton abundance and a species-compositional shift away from dominance by nitrogen-fixing cyanobacteria (Hawes and Smith, 1993).

Grimshaw *et al.* (1993) and Raschke (1993) suggested that increased inflow of dissolved phosphorus into the Florida Everglades is strongly affecting growth and species composition of periphyton in this ecosystem. Grimshaw *et al.* noted strong correlations between water-column phosphorus concentration and the phosphorus content and mean relative abundance of eutrophic algae in the periphyton. Raschke analyzed data collected over a 12-year period to demonstrate increases in water-column phosphorus, increases in phosphorus concentration in the sediment, and an increase in diatom taxa considered to be indicators of phosphorus enrichment. Phosphorus fertilization of a pristine tundra river over four consecutive summers (Peterson *et al.*, 1993a), and $\text{NH}_4\text{-N}$ addition for a single summer at a downstream site on the same river (Peterson *et al.*, 1993b), dramatically changed biological processes and populations at all trophic levels. Carbon and nitrogen stable isotope tracers used in these studies indicated that measured increases in insect and fish growth in fertilized river sections were largely attributable to enhanced epilithic algal production. Ollikainen *et al.* (1993) documented changes in species composition in the benthic diatom community of two large Finnish lakes between 1985 and 1990 that they interpreted as being indicative of the early stages of eutrophication.

Gu and Alexander (1993) used stable isotopes of nitrogen to examine the dynamics of nitrogen supplies to green algae and N_2 -fixing bluegreen algae from arctic and subarctic lakes. N_2 -fixing algae had a higher nitrogen content than nonfixers and obtained most of this (58 to 75%) through fixation of atmospheric nitrogen. Paerl *et al.* (1993a) examined the effect of enrichment by nitrogen, phosphorus, iron, molybdenum, and dissolved organic carbon (DOC) on CO_2 fixation and N_2 fixation in a phys-

iologically diverse suite of marine microbial mats. Results suggested that these communities optimally sequester carbon and nitrogen, thus minimizing limitation by these elements, and are able to accumulate biomass despite the oligotrophic conditions in which they typically reside. Marinelli (1993) conducted chamber experiments to test the effect of two species of polychaete, one a surface deposit feeder and one a head-down deposit feeder, on the flux of silica from the sediments and the effect of such fluxes on benthic diatom activity. Her results indicated that interactions between deposit feeders and benthic microalgae can generate a positive feedback in which activity of deposit feeders increases nutrient availability and stimulates recovery of their microalgal food source.

Photosynthesis, production, and the effects of irradiance. Several studies investigated the effects of solar radiation on various aspects of microalgal primary producers. Donkor *et al.* (1993) discussed the effects of tropical solar radiation on the motility of filamentous cyanobacteria and demonstrated that UV-B, UV-A, and visible light impairs motility in *Anabaena variabilis*, *Oscillatoria tenuis*, and two strains of *Phormidium uncinatum*. Bothwell *et al.* (1993) shielded developing benthic algal communities from ultraviolet (UV) radiation and found that, in the short term (2 to 3 weeks), diatoms within these communities had growth rates 30 to 40% higher than those exposed to natural levels of UV light. As development continued (5 weeks), however, communities exposed to UV supported algal biomass two- to fourfold greater than shielded communities primarily due to a successional shift toward large stalked diatoms in the UV-exposed treatments. Pentecost (1993) suggested that *Rivularia* colonies produced protective extracellular scytonemin pigments in response to UV irradiance. Similarly, Bidigare *et al.* (1993) presented evidence that large accumulations of astaxanthin esters in lipid globules of some species of snow algae provided a photoprotective function by shielding chlorophyll from photoinhibition and photodamage. Ploug *et al.* (1993) used oxygen and light microsenors to discern the role of complementary spectral utilization of light in the zonation of diatoms and cyanobacteria in sediments. The quality of the light that passes through the sediment surface is favorably altered (to 107% the ambient quality) for the underlying cyanobacteria by selective absorption by the overlying diatoms. Vincent *et al.* (1993) observed distinct vertical zonation in pigment distribution within Antarctic cyanobacterial mats, characterized by a carotenoid-rich surface layer overlying a layer of high chlorophyll *a* and phycocyanin concentration. Photosynthetic rates were greatest within these deep chlorophyll-rich zones, and cyanobacterial trichomes residing in these areas migrated to the mat surface in response to reduction in ambient light. Algal standing crop in a stream within a clearcut section of the Hubbard Brook Experimental Forest increased relative to that within a well-shaded reference stream section, in response to increased light availability (Ulrich *et al.*, 1993). Rates of benthic macroalgal production on a temperate continental shelf in Massachusetts Bay were relatively high ($20.9 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$), despite very low ($4.7 \mu\text{E m}^{-2}\cdot\text{s}^{-1}$) irradiance in this habitat (Cahoon *et al.*, 1993).

Effects of environmental conditions on algal or bacterial productivity and photopigments were discussed in several papers. Diel oxygen curves were used to estimate ecosystem gross primary production and community respiration in the river outlet of an eutrophic lake (Uehlinger, 1993). Sun *et al.* (1993) investigated the degradation of chloropigments in anoxic and oxic

sediments in Long Island sound and discussed the pathways of degradation in both oxygen environments. Angradi and Kubly (1993) conducted a series of emersion experiments on *Cladophora*-dominated communities in the tailwaters of Glen Canyon Dam, Arizona, and determined that the extent of chlorophyll *a* degradation, and associated reduction in gross primary production, caused by emersion was directly related to the number of daylight hours to which communities were exposed. Primary productivity per unit chlorophyll was, however, unaffected by exposure length. Pickney and Zingmark (1993b) developed a habitat-specific production simulation model to quantify annual benthic microalgal production in five habitats within an estuary. Short *Spartina*-zone habitats provided 45% of total microalgal annual production, followed by intertidal mudflats (22%), tall *Spartina* zones (18%), shallow subtidal (13%), and intertidal sandflat habitats (3%). Sander and Kalf (1993) reviewed literature on factors controlling bacterial production in marine and freshwater sediments and concluded that substrate supply and temperature are most important in determining bacterial production and specific growth rates. Findlay *et al.* (1993) performed a series of experiments to assess bacterial-algal relationships in streams and concluded that, unlike planktonic systems, no tight trophic connection exists between algal and bacterial productivity in the streams they studied.

Physiological processes within biofilms. The role of extracellular enzymes in biofilms was investigated by several authors. Size fractionation of aminopeptidase activity and incorporation of dissolved substrates were analyzed in a nutrient-poor and two nutrient-rich habitats (Unanue *et al.*, 1993). Their data indicated that bacteria alone could not account for most enzymatic activity in the two nutrient-rich systems. Scholz and Boon (1993c) studied biofilm development on wood substrata in Australian billabongs for 24 weeks and assayed alkaline phosphatase, aminopeptidase, and beta-D-glucosidase activities within the biofilms. Activities of these enzymes differed with season, site, and duration of substratum exposure. Jones and Lock (1993) tracked seasonal changes in extracellular enzyme activity in biofilms from two rivers, one an unshaded oligotrophic stream, the second an eutrophic river with a developed riparian canopy. Per-cell extracellular activities were generally greater at the oligotrophic site. Hantke and Melzer (1993) reported that the ability of the diatom, *Synedra acus*, to take up phosphate varied with pH. At low phosphate concentrations, typical of natural waters, both the half saturation constant and uptake velocity increased with increases in pH from 7 to 9.

A few papers addressed the uptake and production of organics by biofilms or the role of benthic microbiota in nutrient cycling processes. Paerl *et al.* (1993b) characterized the production, uptake, and exchange of several dissolved organic substrates among bacteria and algae within a marine microbial mat. Glucose uptake and the production of CO₂ and short-chain fatty acids were monitored on a seasonal basis in undisturbed cores collected from an intertidal mud flat; monosaccharide uptake rate decreased with sediment depth and varied with temperature (Sawyer and King, 1993). Bastia *et al.* (1993) screened 41 species of filamentous heterocystous blue-green algae for their ability to grow in the light with a photosynthesis inhibitor 3'-(3,4-dichlorophenyl)l',l'-dimethylurea (DCMU) and in the dark on glucose, fructose, and sucrose. Although all species tested demonstrated highest growth rates in the light, 10 species could efficiently use photoheterotrophy and chemoheterotrophy. Gächter and Meyer

(1993) reviewed and analyzed results from published literature on the contribution of bacteria to phosphorus cycling across the sediment/water interface and concluded that bacterial-mediated processes are important in sediment phosphorus release and retention, particularly in oligotrophic lakes. Fenchel (1993) described the relatively small role that anaerobic protozoa with endosymbiotic methanogenic bacteria play in the process of methane production in sediments as a result of their higher trophic position in an ecosystem with low growth efficiencies. The coupling of microbial fermentation and respiration processes in intertidal mudflat sediments was studied by Kerner (1993). On an annual basis, reduction of manganese, ferric iron, and oxygen were maximal in early summer, and fermentation-derived CO₂ was the same magnitude as that for oxygen respiration in summer.

Hoagland *et al.* (1993) synthesized current knowledge of function, fine structure, chemistry, and physiology of diatom-produced extracellular polymeric substances. Several other papers investigated properties of the exopolymer-laden biofilms produced by *Pseudomonas aeruginosa*. The transport of fluorescent latex particles (1 µm diam) into a *P. aeruginosa* biofilm was determined by microscopic examination of thin cross-sections of embedded biofilm (Drury *et al.*, 1993). Particles penetrated the biofilm and remained in it much longer than predicted by an existing mathematical model. Vandevivere and Kirchman (1993) demonstrated that the introduction of solid surfaces (sand grains) to bacterial cultures can stimulate attached bacteria to produce exopolysaccharides without changing the specific growth rate, growth stage, or limiting nutrient. Davies *et al.* (1993) showed that expression of a gene (*algC*) for production of the exopolymer alginate was higher for *Pseudomonas aeruginosa* exposed to a Teflon mesh attachment surface than for nonattached cells.

Decomposition of organic matter and the function and distribution of aquatic fungi. Research on the process of organic matter decomposition in aquatic ecosystems was conducted by several authors. Ostrofsky (1993) examined the tannin content of autumn-shed leaves of 48 deciduous trees. Tannin concentrations did not correlate to published rates of leaf processing or to microbial colonization, suggesting that the large variation seen in leaf-processing rates is not due to tannin concentration but to abiotic factors such as leaching and physical fragmentation. Degradation of pre- and postbloom water hyacinth leaves was investigated by Singhal *et al.* (1993) under laboratory conditions. Leaching accounted for most of the decomposition within the first 4 days, whereas decomposition by microbial activity increased exponentially in the later phase of decay. Tanaka (1993) conducted a litter bag experiment in an eutrophic seawater lake from autumn to summer and determined that *Pseudomonas* was the most important bacterial genus (accounting for 65 to 90% of total cellulolytic bacteria) on decomposing *Phragmites communis* leaf litter.

Several papers addressed the function and distribution of aquatic fungi or their role in decomposition of organic matter in lakes and streams. Chergui and Pattee (1993) investigated fungal and invertebrate colonization of fresh and dry willow (*Salix*) leaves in two lotic systems. Fresh leaves contained antifungal substances that delayed fungal colonization; these substances were rapidly leached from dried leaves. Sridhar and Bärlocher (1993) also found that aquatic hyphomycetes colonized dried leaves more quickly than fresh leaves, but, despite this,

fresh leaves were preferred by two stream invertebrates. Further, concentrations of extractable protein decreased with leaf age, and fungal colonization and shredder consumption was usually positively correlated with protein content of the leaves. Newell and Bärlocher (1993) demonstrated that shredding activity by snails on decaying cordgrass affected fungal standing crops and fungal community dynamics in cordgrass marshes. Ecological observation on aquatic hyphomycetes in the Cauvery River (India) and its tributaries were made by Rajashekhar *et al.* (1993); the occurrence of several species of fungi was related to rainfall, total hardness, pH, and dissolved oxygen. Mansfield and Bärlocher (1993) described the seasonal variation of fungal biomass on balsawood panels buried in anaerobic salt marsh sediments. Eight fungal species isolated from nearby *Spartina alterniflora* roots did not grow in anoxic environments. Gönczöl and Révay (1993) conducted a 2-year study of the longitudinal distribution and colonization patterns of fungi on twigs in a Hungarian stream. Species composition, diversity, and fungal activity appeared to be strongly influenced by location of twigs in the stream. Successional patterns in aquatic hyphomycete assemblages on alder leaves in a stream was studied for 2 successive years (Gessner *et al.*, 1993). Early-, intermediate-, and late-successional assemblages were identified, and this floristic pattern was similar between seasons and successive years. Microbial respiration, measured on twigs and leaves of rhododendron and birch, was compared among four headwater stream sites in North Carolina (Tank *et al.*, 1993). Although the decay rate of birch > rhododendron > twigs, mean respiration rates per unit surface area of substrata were highest for twigs, followed by rhododendron and then birch, indicating that substrata stability and persistence may affect microbial respiration. Sinsabaugh *et al.* (1993) investigated the relationship between ectoenzyme activity of epixylic microbes with decomposition rates, substrate quality, and nutrient availability by placing stick substrata in several lotic systems in upstate New York for 3 years. They proposed an economic model that directly links nitrogen and phosphorus availability to litter decomposition rates on the basis of microbial extracellular enzyme production.

Miscellaneous. Accumulation of cobalt and cesium by a Chlorophyte (*Scenedesmus obliquus*) and a cyanobacterium (*Synechocystis*) was characterized at metal concentrations of 1 to 100 μM in the presence of montmorillonite, illite, and kaolinite clays (Garnham *et al.*, 1993). Metal accumulation varied with external pH and NaCl concentration and differed based on the species involved and the proportion of clay in clay-algal aggregates. Dakhama *et al.* (1993) reported that the phenazine pigments, 1-hydroxyphenazine and oxychlororaphine, released by the bacterium, *Pseudomonas aeruginosa*, strongly inhibited growth of a number of green microalgal and cyanobacterial species. The diplobiontic life cycle of the freshwater green alga, *Rhizoclonium hieroglyphicum*, was described and illustrated by Parodi and Cáceres (1993). Mann (1993) discussed variations in sexual reproduction among diatoms of different taxonomic affinities and speculated on the evolutionary implications of these differences. DeLong *et al.* (1993) used molecular techniques to demonstrate that marine bacterioplankton are phylogenetically distinct from bacteria associated with phytodetrital aggregates co-occurring in the same water mass. Poff *et al.* (1993) characterized the size structure of the entire metazoan community of a fourth-order, sandy-bottom Piedmont stream. Calculation of size-specific contributions to whole-community metabolism

yielded a bimodal distribution, with meiofauna (mostly oligochaetes and microcrustaceans) accounting for one of the two peaks.

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Effects of chemicals on microorganisms

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Microbial responses to chemicals manifest themselves in a variety of forms depending on the chemical, the type of microorganism, the concentration, the exposure time, and other chemical, physical, biological, and environmental factors. Barriers to quantifying the effects of chemicals on microorganisms are frequently related to methodological or analytical limitations. Recent developments in methodologies used to evaluate chemical-microbial interactions are summarized in this paper. A brief overview of recent studies on microbial responses to specific chemicals is provided in tabular form categorized by chemical and microorganism.

Editor's Note: Because this topic was not included in the 1993 Literature Review issue, this year's review covers literature from a 2-year period.

MEASUREMENT METHODS

A summary of methodologies used to evaluate the effects of chemicals on microorganisms is given in Table 1. The tests vary in terms of the organism used, the analytical techniques, the sensitivity, and time required. In some cases comparisons were made among several types of testing, whereas in many cases one type of test was used to compare responses to different chemicals.

EFFECTS OF ORGANIC CHEMICALS ON MICROORGANISMS

Studies in which the effects of organic chemicals on microorganisms were quantified are summarized in Table 2. The table is organized alphabetically by type of organism and grouped alphabetically by the chemical name. The majority of the studies were conducted using bacteria, with some studies based on algae as test organisms, and some studies based on fungi and protozoa.